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Hydroperiod and Its Influence on Nekton Use of the Salt Marsh: A Pulsing Ecosystem

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ABSTRACT: The salt marsh surface is not a homogeneous environment. Rather, it contains a mix of different microhabitats, which vary in elevation, microtopography, and location within the estuarine system. These attributes act in concert with astronomical tides and meteorological and climatological events and result in pulses of tidal flooding. Marsh hydroperiod, the pattern of flooding events, not only controls nekton access to marsh surface habitats directly but may also mediate habitat exploitation through its influence on other factors, such as prey abundance or vegetation stem density. The relative importance of factors affecting marsh hydroperiod differ between the southeast Atlantic and northern Gulf of Mexico coasts. Astronomical tidal forcing is the primary determinant of hydroperiod in Atlantic Coast marshes, whereas predictable tides are often overridden by meteorological events in Gulf Coast marshes. In addition, other factors influencing coastal water levels have a proportionately greater effect on the Gulf Coast. The relatively unpredictable timing of marsh flooding along the Gulf Coast does not seem to limit habitat utilization. Some of the highest densities of nekton reported from salt marshes are from Gulf Coast marshes that are undergoing gradual submergence and fragmentation caused by an accelerated rise in relative sea level. Additional studies of habitat utilization are needed, especially on the Pacific and Atlantic coasts. Investigations should include regional comparisons of similar microhabitats using identical quantitative sampling methods. Controlled field experiments are also needed to elucidate the mechanisms that affect the habitat function of salt marshes.

Introduction

Mitsch and Gosselink (1986) identify hydrology as possibly the most important factor affecting the establishment of wetlands and regulation of wetland processes. Pulses of tidal flooding, which characterize the hydrology of estuarine marshes, drive a multitude of wetland functions, including the exchange of nutrients, sediments, organic material, and biota between the marsh and the rest of the estuary. The hydrology of each estuarine marsh produces a characteristic hydroperiod or pattern of marsh flooding. The hydroperiod can be represented graphically by plotting changes in water level over time and marsh surface elevation (Mitsch and Gosselink 1986). By comparing these variables (water level and marsh elevation) within a given time period, the frequency (number of flooding events per unit time) and duration (proportion of time an area is inundated) of marsh flooding can be determined.

Marsh hydroperiod obviously controls habitat use by nekton, because most natant organisms can occupy the marsh surface only when it is flooded. Studies have documented direct use of the marsh surface in several coastal areas and a wide range of salinity regimes (Zimmerman and Minello 1984; Rozas and Odum 1987; McIvor and Odum 1988; Hettler 1989; Kneib 1991; Murphy 1991; Baltz et al. 1993). Studies of salt marshes in the southeast region of the United States have documented the presence of at least 51 species in 24 families of fishes and seven species in three families of decapod crustaceans in marsh-surface habitats (Rozas 1993). Nekton assemblages associated with the marsh surface are numerically dominated by resident estuarine species. However, seasonal pulses of transient estuarine species are regularly recruited to marsh-surface habitats from nearshore spawning areas, and many of these species support important commercial fisheries.

Most research examining habitat utilization of estuarine marshes has focused on frequently flooded salt marshes of the southeast region of the United States (Rozas 1993). This region includes the estuaries along the northern Gulf of Mexico and the southeast Atlantic coasts and contains 78% of the coastal wetlands in the United States (Gosselink and Baumann 1980). Salt marshes of the region are most extensive on the Gulf Coast in the

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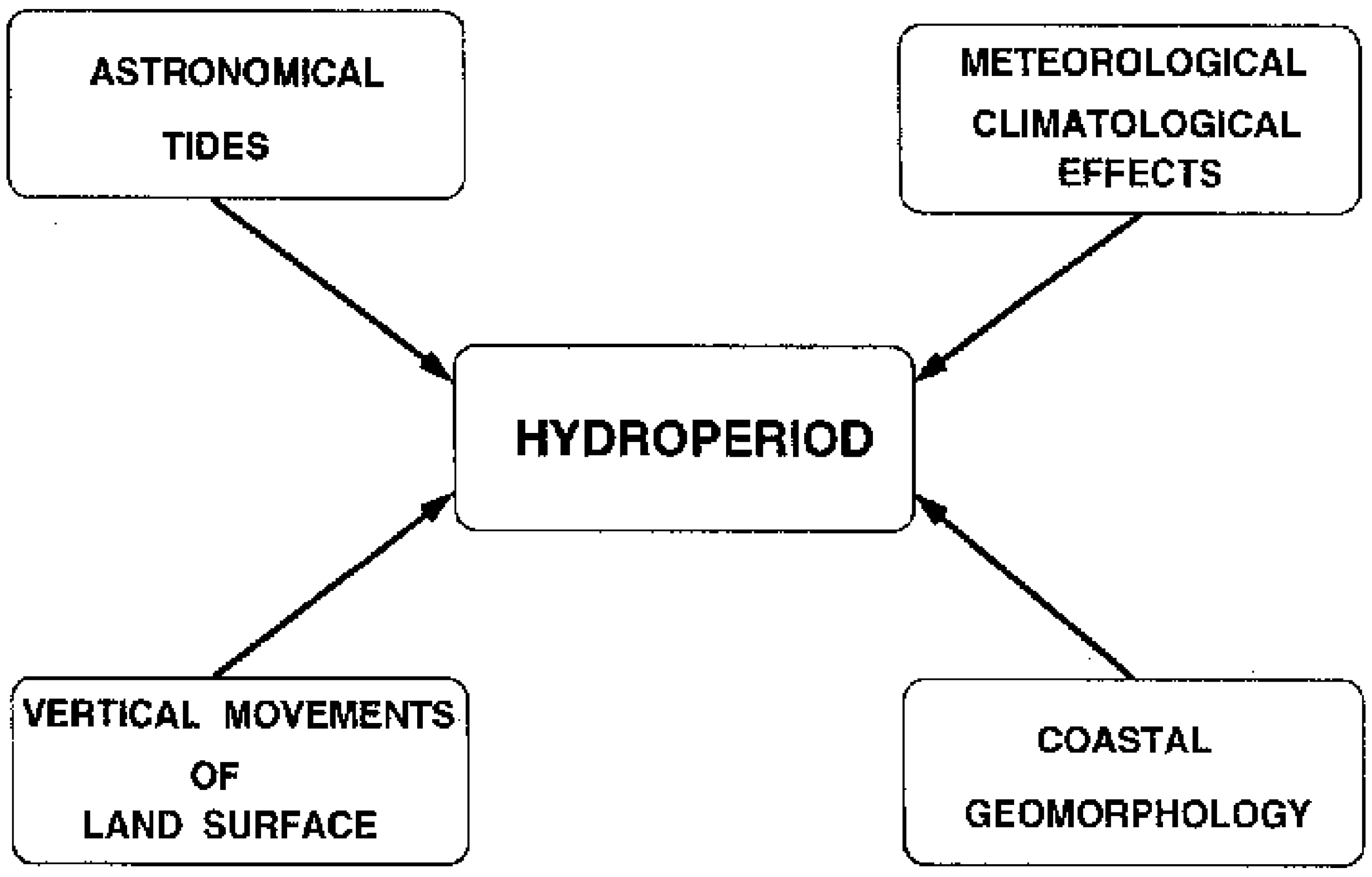

Fig. 1. Factors that influence the hydroperiod of any tidal salt marsh can be assigned to one of four major types.

Mississippi River deltaic plain of Louisiana and on the Atlantic Coast bordering the estuaries of Georgia and South Carolina. The hydrology of these two coasts differs, not only in tidal frequency and amplitude, but also in the influence of such factors as weather, seasonal changes in mean sea level, and the rate of relative sea-level rise. Therefore, the hydroperiods of salt marshes in the two areas are different.

The species assemblages of frequently flooded salt marshes in the two regions are very similar. The marsh vegetation is dominated by smooth cordgrass, *Spartina alterniflora* Loisel, in association with *Juncus roemerianus* Scheele, *Distichlis spicata* (L.) Greene, and *Spartina patens* (Aiton) Muhl. In addition, assemblages of nekton, epibenthos, and benthic infauna inhabiting salt marshes on the two coasts are composed of the same or closely related species (Heard 1982; Williams 1984; Robins et al. 1986).

The goals of this paper are to describe the factors that affect the hydroperiod of frequently flooded salt marshes in the southeast region of the United States and the time scales of flooding events, to discuss the influence of marsh hydroperiod on habitat function in the region, to compare marsh hydroperiod and habitat utilization between the two coasts in the region, and to briefly discuss future research needs.

Factors Determining Salt Marsh Hydroperiod

The hydroperiod within a salt marsh is controlled by numerous factors that can be grouped into four major categories (Fig. 1). The degree to which these factors influence marsh hydroperiod differs between the northern Gulf of Mexico and southeast Atlantic coasts.

Astronomical Tides

Astronomical tides inundate regularly flooded coastal marshes either daily (diurnal tides) or twice daily (semidiurnal tides) during most of the year. The tidal magnitude depends most on the phase of the moon, declination of the moon relative to the equator of the Earth, and the position of the Earth relative to the Sun. Whether marshes within a region experience daily or twice-daily tides depends on the relative strengths of five major constituents (three semidiurnal and two diurnal) of the astronomical tide (Marmer 1954). The semidiurnal constituents dominate along the Atlantic Coast, and tides there are mesotidal in magnitude. Thus, this coast experiences twice-daily astronomical tides of a meter or more, with tidal amplitude dependent largely on the phase of the moon. Highest monthly tides occur during full and new moons (spring tides), whereas lowest tides coincide with quarter phases of the moon (neap tides). Estuaries on the Atlantic Coast (except those with few inlets and greatly restricted tidal exchange) experience average tidal amplitudes as high as 1.2 m to 2.3 m (Dardeaux et al. 1992).

By comparison, tides along most of the Gulf of Mexico coast are microtidal (<1 m). Because the magnitudes of the diurnal constituents are much greater than those of the semidiurnal constituents (except the northern coast of Florida from Apalachee Bay to near Tampa Bay), tides in this region are predominately diurnal, and the declination of the moon has the greatest effect on tidal amplitude (Marmer 1954; Ward 1980). For example, along the Texas coast, tidal amplitudes range from 0.8 m at maximum declination (tropical tides) to 0.2 m at minimum declination (equatorial tides) (Ward et al. 1980).

Tidal range also varies interannually over the 18.6-yr lunar epoch due to changes in the inclination of the moon's orbit relative to the Earth's equator. The amplitude of semidiurnal tides increases as the inclination of the moon's orbit decreases; the response of diurnal tides is greater and in the opposite direction (Marmer 1954).

Meteorological/Climatological Effects

Sustained winds along coastal ocean waters or a coastal bay may cause changes in estuarine water levels. Wind stress that forces ocean waters onshore tends to raise (setup) estuarine water levels as seawater is driven in from the ocean. Winds that drive coastal waters offshore have the opposite effect; they lower (setdown) estuarine water levels.

Meteorological forcing may affect marsh hydroperiod quickly over periods as short as several hours (due to diurnal changes in wind speed and direction), but the most important effects of wind stress occur at longer time scales. Strong sustained winds associated with tropical storms, for example, cause some of the greatest increases in coastal water levels. Water levels in the vicinity of hurricane landfall may exceed normal tides by several meters (Chabreck and Palmisano 1973). However, in any given year, the probability of such a storm affecting an individual estuary is relatively low (Simpson and Lawrence 1971).

Although cold fronts (extra-tropical storms) usually have a less dramatic effect on coastal water levels, they have a stronger influence on marsh hydroperiod, as they occur much more frequently, and each event affects a larger coastal area than tropical storms. Cold fronts are especially important in microtidal environments because their effect on water levels often exceeds that of astronomical tides, especially when frontal passage coincides with equatorial tides (Smith 1979; Ward 1980; Swenson and Chuang 1983; Pietrafesa and Janowitz 1988). The passage of cold fronts largely controls marsh hydroperiods along the northern Gulf of Mexico from October through March, over time scales of 3–6 d (Smith 1978).

The effect of cold fronts on marsh hydroperiod is illustrated in Fig. 2, which depicts the tidal record for portions of spring and summer 1993 recorded at a site in upper Galveston Bay. In spring, the effects of passing cold fronts dominate the hydrograph (Fig. 2a). Strong southerly winds may precede a front's arrival by several days, completely overriding any influence of the astronomical tide, and substantially increasing the flooding duration of coastal marshes (Fig. 2a). Following frontal passage, the abrupt shift in wind direction to the north and rise in barometric pressure cause water levels to drop and result in rapid draining of tidal marshes (Smith 1979; Ward 1980). With frontal passage and sustained northerly winds, water levels in the upper estuary may drop more than 1 m in a few hours (Orlando et al. 1991). Compare the hydrograph for April, when the astronomical tidal signal was completely obscured in most of the record, to water-level fluctuations recorded in July when frontal activity was absent (Fig. 2b). The predominantly diurnal astronomical tidal signal that characterizes Gulf Coast estuaries is clearly visible in Fig. 2b.

The response of marsh water-levels to wind stress may vary in magnitude and even direction depending on the location of the marsh within the estuary. Because wind stress tilts the water surface across an estuary, it may simultaneously depress water levels along the upwind shore and raise them at the downwind shore. Thus, water levels in marsh along one shoreline will respond differently to the same wind stress than water levels in marsh along the opposite shoreline. This phenomenon is most pronounced in estuaries with restricted inlets, where wind stress associated with the passage of cold fronts may cause a seiche effect much like that of an enclosed waterbody (Ward 1980).

Alongshore wind stress also affects water levels on the southeast Atlantic Coast (Chao and Pietrafesa 1980), but the response of estuarine water levels to north-south wind stress is opposite that observed on the Gulf Coast (Pietrafesa and Janowitz 1988). South to southwest winds cause a drop in coastal sea-level, whereas north to northeast winds cause a rise in sea level because of coastal Ekman transport (Kjerfve et al. 1978; Wang and Elliot 1978; Pietrafesa and Janowitz 1988). As on the Gulf Coast, the most important meteorological forcing event along the southeast Atlantic is the passage of cold fronts. These storms are sometimes referred to as "noreasters" because the low pressure systems associated with cold fronts tend to track northeast along the Atlantic Coast. Northerly winds associated with the passage of winter storms may persist for 2–10 d, causing setup in estuaries and increasing marsh hydroperiods and flooding depths (Pietrafesa and Janowitz 1988). An example of water-level fluctuations induced by meteorological forcing is given by Pietrafesa and Janowitz (1988) for the Cape Fear River estuary, North Carolina. Although this type of meteorological forcing is less dramatic relative to astronomical tides in the mesotidal and macrotidal environments along the Atlantic Coast, wind effects may dominate in this region during neap tides (Boon 1975) or in estuaries where restricted tidal exchange between ocean and estuary creates a microtidal environment, for example, Albemarle Sound (Giese et al. 1979).

Seasonal shifts in the direction and magnitude of prevailing winds also have an effect on estuarine water levels and marsh hydroperiod (Smith 1978; Pietrafesa and Janowitz 1988; Orlando et al. 1991). Changes in monthly mean water-levels are thought to be caused by seasonal shifts in prevailing winds as well as the seasonality of freshwater discharge from major rivers and oceanic heat storage (Pattullo et al. 1955; Meade and Emery 1971; Sturges and Blaha 1976). Monthly mean water-levels vary by approximately 0.25 m along both the Atlantic and Gulf coasts (Patullo et al. 1955). Along most of the Atlantic Coast, water level is lowest early in the year (winter or spring), gradually rises to a peak in fall, and then subsides through the rest of the year. For example, departures from the annual mean water-level at Charleston, South Carolina, are −8.7 cm in January and +17.3 cm in October

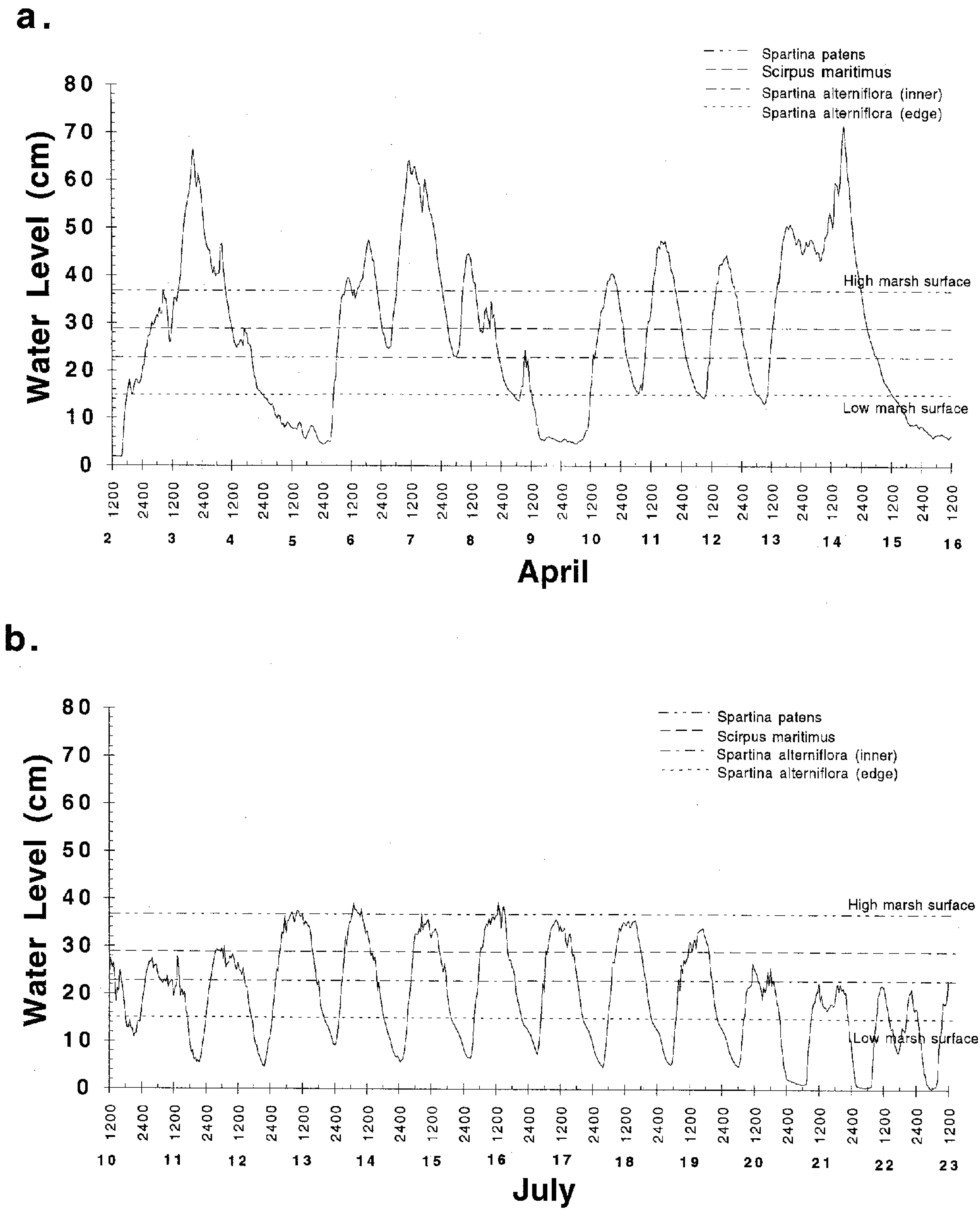

Fig. 2. Hydroperiods of four marsh types at Atkinson Island in upper Galveston Bay for (a) April 2–16 when the tidal signal during most of the period was driven by wind and barometric pressure changes associated with the passage of three cold fronts (fronts crossed the Texas coast April 4, 8, and 15) and (b) July 10–23 when astronomical tides predominated.

(Patullo et al. 1955). Similarly, along most of the northern Gulf Coast the water level is lowest in winter and highest in fall, but a secondary positive departure from mean water level occurs during spring. For example at Galveston, Texas, departures of −11.2 cm, +5.9 cm, and +13.2 cm are observed in January, May, and September, respectively (Patullo et al. 1955). Although the magnitude of departures in the Gulf and Atlantic regions are similar, the effect on marsh hydroperiod is much more significant in Gulf Coast estuaries where the seasonal variation in water level is the same order of magnitude as the average daily tidal range (Provost 1976). Such a range in monthly mean water-level represents <25% of the daily tidal range along much of the Atlantic Coast.

Long-period fluctuations in coastal water-level and marsh hydroperiod can result from changes in weather patterns or climatic changes occurring at frequencies of years to centuries or more. For example, Childers et al. (1990) postulate that El Niño-Southern Oscillation events, which occur at frequencies of 2–7 yr, cause increased flooding of coastal marshes in Louisiana by increasing the rate of precipitation both locally and in the Mississippi River basin. In contrast, La Niña events generate dry conditions, which lower water levels and decrease marsh flooding in Louisiana (Childers et al. 1990). Such fluctuations in mean annual sea-level are known to occur on the Atlantic Coast as well, and the magnitude of the deviation from the long-term mean is on the order of 10 cm for both regions (Childers et al. 1990; Morris et al. 1990).

Although year-to-year changes in sea level may be either positive or negative, the long-term trend is one of a gradual eustatic rise in mean sea level thought to be caused by climatic warming, melting of the polar ice caps, and the resulting increase in oceanic water volume (Gornitz et al. 1982). However, in the context of late Holocene sea-level rise, the current rate (0.12 cm yr^{-1}) is relatively small (Gornitz et al. 1982), and long-term changes in marsh inundation depend upon vertical movements of the land surface as well as eustatic changes in sea level. This absolute vertical relationship between water and land is termed relative sea-level (Penland and Ramsey 1990). Rates of relative sea-level rise vary among regions of the United States (Stevenson et al. 1986), but in some areas, especially along the Gulf Coast, marsh hydroperiods have been substantially increased by this phenomenon (Penland and Ramsey 1990).

Vertical Movements of Land Surface

Marsh hydroperiod is not only affected by local tidal regime and all the factors that influence it, but it is also determined by changes in surface elevation. The direction and magnitude of elevational changes in coastal wetlands vary regionally as do their causes (Stevenson et al. 1986). Most of the Atlantic Coast is relatively stable, although some marshes of Chesapeake Bay are undergoing submergence and experiencing increasing hydroperiods because accretion is not compensating for local subsidence (Holdahl and Morrison 1974; Stevenson et al. 1986). The highest reported rates of coastal submergence are for the northern Gulf Coast in Texas and Louisiana (Penland and Ramsey 1990). In Galveston Bay, Texas, compactional subsidence caused by belowground fluid withdrawal and subsidence along active surface faults have caused high submergence rates in marshes (White et al. 1993). The rate of relative sea-level rise is even higher in Louisiana; in Terrebonne Parish, for example, the rate is 1.19 cm yr^{-1}, 10 times the world average (Penland and Ramsey 1990). This rapid rate of coastal submergence in southeast Louisiana is mainly the result of delta subsidence, which is part of the natural deltaic cycle, and a sediment deficit caused by human activities that curtailed inputs from the Mississippi River to deltaic wetlands (Baumann et al. 1984; Penland and Ramsey 1990).

Plants and animals may influence marsh hydroperiod by altering marsh-surface topography (Odum 1989). Plants stabilize the marsh substrate, facilitate sediment accretion, and add organic matter to sediments (Reed and Cahoon 1992). Therefore, in vertically stable areas (no subsidence) the presence of vegetation may gradually reduce hydroperiod by raising marsh elevation (Osgood and Zieman 1993). Intense herbivory, which completely removes the vegetation from the marsh surface (Lynch et al. 1947; Smith and Odum 1981), may enhance erosion and increase hydroperiod (Llewellyn and Shaffer 1993). Other types of animal activity, including that of fiddler crabs, mussels, and small mammals, may alter the frequency and duration of marsh flooding by modifying the local microtopography (Bertness 1984; Odum 1989; Reed 1989). Although these activities cause relatively small changes in marsh surface topography, differences of only a few centimeters in microtidal environments may cause substantial variations in local inundation regimes (Reed 1989; Rozas and Reed 1993). In a Louisiana salt marsh, a difference in elevation of only 12 cm caused flooding durations in 1988 to vary from 21% of the time at the highest topographic sites to 53% of the time at lowest sites (Reed 1989).

Coastal Geomorphology

As ocean tides propagate into estuaries, they are modified by such factors as inlet configuration, estuary and wetland geomorphology, and local site characteristics. Usually the tide is lagged and diminished in amplitude as it passes through an inlet and travels up the estuary (Smith 1974; Ward 1980). The degree to which the tidal crest is diminished depends on the dimensions of the inlet and the relative size of the estuary. Where communication between estuary and ocean is limited to one or only a few inlets having a small flow capacity relative to the volume of the estuary, tides may be greatly dampened (e.g., Albemarle Sound, North Carolina, and San Antonio Bay, Texas) (Ward 1980). The dependence of tidal amplitude on inlet dimensions is illustrated by changes in the Cape Fear River estuary that followed enlargement of the ship channel. Hackney and Yelverton (1990) attributed a 67% increase in the tidal amplitude at the upper reach of the estuary to the enlarged dimensions of the inlet, which allowed a larger volume of water to be carried into the estuary with each flood tide. With the resulting rise in high-water datums and increased salinity in the estuary, tidal marshes have expanded into areas historically occupied by tidal swamps (Hackney and Yelverton 1990). Although increasing the capacity of an inlet to convey tidal waters usually increases the tidal amplitude in the estuary, it may also lower mean water-level in the upper estuary (Marmer 1977).

The geomorphology of the estuary may also increase tidal amplitude by constricting and magnifying the tide in the upper estuary. This phenomenon may compensate for tidal amplitude attenuation that occurs as the tide travels through an inlet and up the estuary. Such is the case in some tributaries of upper Chesapeake Bay, where tidal amplitudes, even at locations hundreds of kilometers from the coast, are similar to the tidal range found at the mouth of the estuary. Estuarine geomorphology and bathymetry influence water levels in other ways as well. For example, estuaries with a large surface-area-to-volume ratio are generally more susceptible to meteorologically-induced changes in water level (Ward 1980).

Local site attributes also may influence marsh hydroperiod. The effect that distance from the ocean has on tidal attenuation and marsh hydroperiod has already been discussed, but nearness to a large river can also affect water levels in a marsh. Marshes on active river deltas or those located near a major river mouth may have hydroperiods that are greatly influenced by seasonal changes in river discharge (Marmer 1954). Delta marshes may be continuously inundated for extended periods during floods. The hydroperiod of a site is also influenced by its location within a marsh system. The tidal amplitude is always greater at the mouth of a tidal channel than at the headwater tributaries of

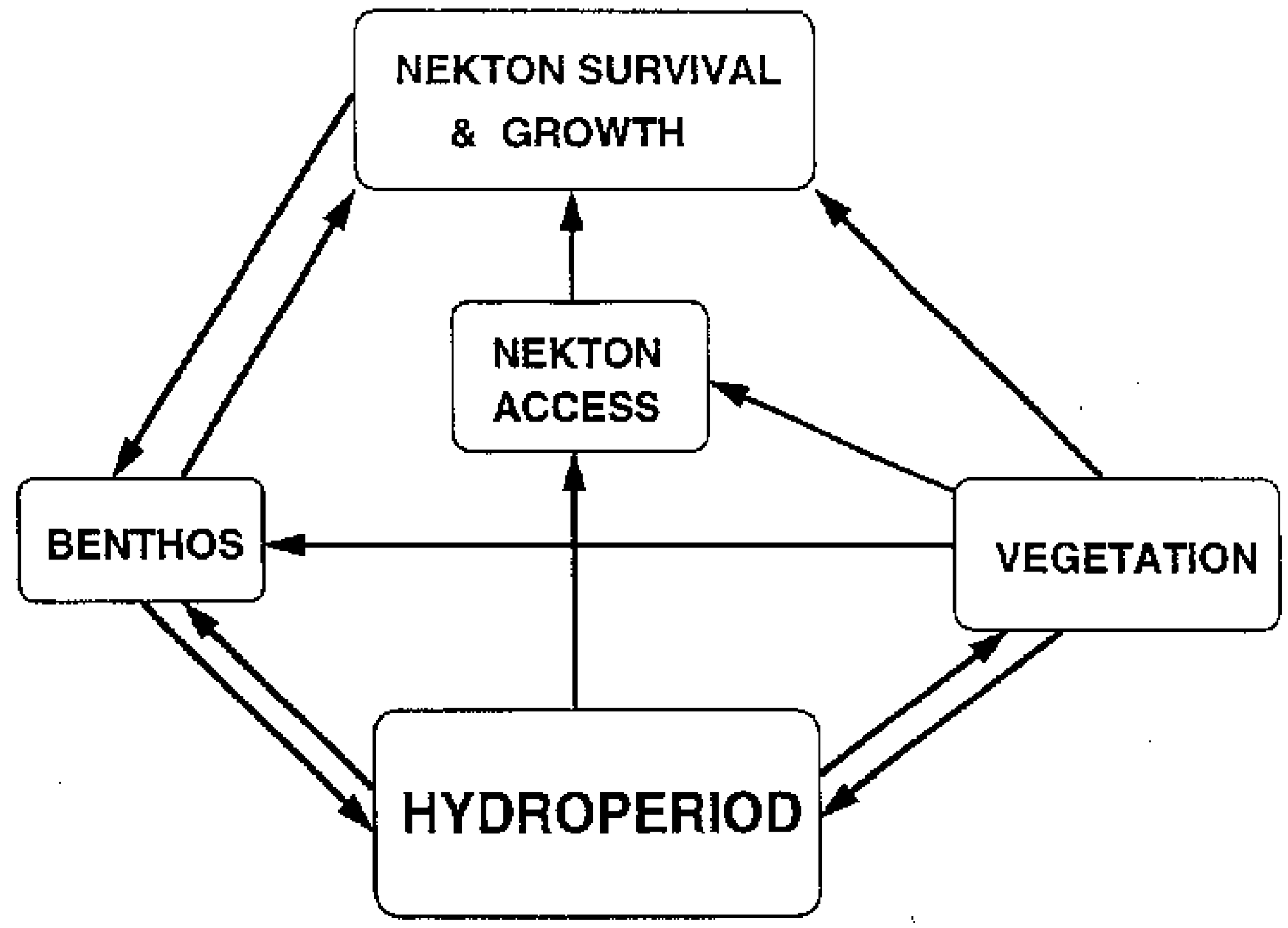

Fig. 3. Marsh hydroperiod may affect the survival and growth of nekton both directly by influencing their access to the marsh surface and indirectly through its effect on vegetation and benthic organisms. Marsh plants and benthic animals may affect hydroperiod by causing changes in surface elevation.

the marsh system (Eiser 1984). Even so, in marshes with a well-developed system of tidal channels (e.g., southeast Atlantic Coast), flooding of the marsh surface usually occurs first at the heads of first-order creeks where creek levees are not well developed (Boon 1975; Collins et al. 1987). Other site properties such as vegetation stem density, plant architecture, and microtopographic relief may also influence marsh hydroperiod. Vegetation and microtopographic resistance impede the flow of water on the marsh surface, delaying both the onset of flooding during a rising tide and marsh drainage as the tide ebbs (Borey et al. 1983; Eiser 1984).

Influence of Hydroperiod on Biota

Hydroperiod profoundly influences both the structure and function of estuarine wetlands. It directly affects nekton use of the marsh surface by controlling access to the habitat, and also may indirectly mediate habitat use through its influence on marsh vegetation and the prey of nektonic predators (Fig. 3).

Plant Community

Within a geographic region, hydroperiod is second only to salinity in importance as a determinant of vegetation composition in estuarine marshes (Mitsch and Gosselink 1986; Latham et al. 1994). For example, marshes of the southeast region within the same salinity regime as *Spartina alterniflora*-dominated marsh but which experience shorter hydroperiods (higher surface elevation) are usually dominated by *Juncus roemerianus, Distichlis spicata,* or *Spartina patens* (Sasser 1977). Each of these species possesses a characteristic growth form and plant architecture. Therefore, by affecting vegetation composition, hydroperiod also influences the structure of the marsh itself. In general, stem density decreases with increasing hydroperiod not only because *S. alterniflora* replaces other more densely growing species on frequently flooded marshes, but also because the density of *S. alterniflora* decreases with flooding duration (Mendelssohn and Seneca 1980; West and Williams 1986; Mendelssohn and McKee 1988; Reed and Cahoon 1992).

Both the total area of intertidal marsh in an estuary and the location of plant species along an elevation gradient within the intertidal zone are closely linked to hydroperiod. This relationship between hydroperiod and the distribution of intertidal vegetation is illustrated by changes in the Oosterschelde (The Netherlands) that followed installation of a barrier restricting tidal flow into the estuary. The barrier reduced the tidal range and mean high water-level to about 88% of their original values in the estuary; 4 yr after the barrier was constructed, most species of salt-marsh vegetation had moved down the elevation gradient and the total area of low marsh had measurably decreased (De Jong et al. 1994; De Leeuw et al. 1994). Because the elevational range at which a species occurs varies directly with tidal amplitude, the elevational range at which *S. alterniflora* grows is much narrower on the Gulf Coast than the Atlantic Coast (McKee and Patrick 1988). McKee and Patrick (1988) reported a relationship between mean tide range and elevational growth range that predicts a relatively narrow growth range (<0.5 m) for *S. alterniflora* on the Gulf Coast and in other microtidal areas. According to this relationship, the growth range of *S. alterniflora* in Atlantic Coast marshes with a mean tidal range of 2 m would be three times the range in Gulf Coast marshes.

Natant organisms using the marsh surface are affected both directly and indirectly by marsh vegetation. Plants afford nekton with cover and protection from large predators (Minello and Zimmerman 1983; Minello et al. 1989). The plant community may also affect the growth and survival of nekton through its influence on the benthic community (infaunal and epifaunal invertebrates). The benthic community, a major source of food for nektonic predators, depends on marsh plants to provide food (detritus) and suitable habitat. Marsh vegetation provides hiding places for benthic prey, and may diminish the foraging efficiency of nektonic predators (Vince et al. 1976; Van Dolah 1978).

Benthic Community

Numerous studies have documented relationships between surface elevation (or flooding duration) and the spatial distribution of marsh infauna and epifauna (Teal 1958; Cammen 1976; Fell et al. 1982; Kneib 1984, 1992; Bishop and Hackney 1987). The distribution of these animals along an elevation gradient is influenced by both physical and biological factors that are mediated by hydroperiod (Kneib 1984; West and Williams 1986). Few aquatic organisms can withstand the harsh physical conditions characteristic of high-marsh environments, which may experience long periods without flooding (Bishop and Hackney 1987; Hummel et al. 1988, 1994; Fortuin et al. 1989). Animals inhabiting marshes with frequent and long periods of inundation are less likely to experience desiccation and exposure to extreme temperatures but may be exposed to greater predation pressure from natant predators (Kneib 1984; West and Williams 1986; Bishop and Hackney 1987; Lin 1989). However, increased predator access may actually enhance some benthic populations in frequently flooded marsh by reducing the number of intermediate predators in the food chain (Kneib and Stiven 1982; Kneib 1988). Prey populations in low marsh may also be replenished more rapidly because the habitat is flooded more frequently and longer than high marsh (Kneib 1993). A complication in the relationship between elevation and predator access is that "distance to a subtidal area" also may be an important factor. Animals tens of meters from subtidal habitat may be subject to less predation than those living at the same elevation near the marsh-water edge because predators may be impeded by dense vegetation; alternatively, the risk of stranding may limit the distance predators will travel into the marsh from permanently-flooded habitat (Gibson 1988; Lin 1989; Minello et al. 1994; Peterson and Turner 1994; Schindler et al. 1994).

Hydroperiod also may indirectly influence benthic organisms through its effect on sediment conditions and marsh vegetation as described above. Many benthic macrofaunal species are closely associated with the culms, roots, and rhizomes of marsh plants. Rader (1984) and LaSalle and Rozas (1991) found higher densities of benthic infauna associated with marsh plants than in adjacent bare areas. Bivalve densities on the marsh surface also were positively related to plant stem density (West and Williams 1986; Capehart and Hackney 1989). Minello and Zimmerman (1992) found that densities of polychaetes and amphipods were positively correlated to the combined biomass of roots, rhizomes, and detritus in the sediment of transplanted salt marshes in Texas. Plants also may serve as stable sites of attachment for tubiculous animals (LaSalle and Rozas 1991). The presence of plants may increase the volume of oxygenated sediments in the root zone and thus expand the habitat available for animals that require aerobic conditions (Teal and Kanwisher 1966; Osenga and Coull 1983). In addition, plants add organic material to sediments and provide a food supply for deposit-feeding infauna (Moy and Levin 1991).

NEKTON COMMUNITY

Because occupation of the marsh surface by most natant organisms (fishes, crabs, and shrimps) is restricted to periods of inundation, hydroperiod controls access to the habitat. Therefore, frequently flooded marshes that experience extended periods of submergence would seem to offer the greatest opportunity for exploitation by nekton. To examine whether submergence time is important in influencing habitat selection on the marsh surface, Rozas and Reed (1993) estimated densities of natant species in three habitats having different elevations (high *Distichlis* marsh, medium *Spartina* marsh, and low *Spartina* marsh) within a Louisiana marsh system. When all three habitats were available for exploitation at high tide, penaeid shrimp concentrated in the low *Spartina* marsh, which flooded longer and more deeply than the other two habitats sampled (Rozas and Reed 1993). Other species also may exploit low *Spartina* marsh early or late in the tidal cycle or during neap or equatorial tides when higher marsh habitat is unavailable.

Long periods of marsh submergence should benefit organisms that forage and seek refuge on the marsh surface, especially when food and cover are less abundant in subtidal habitats (Weisberg and Lotrick 1982; Minello and Zimmerman 1991). Kneib (1993) found that growth rates of larval mummichogs, *Fundulus heteroclitus,* were positively related to flooding duration in a Georgia salt marsh, whereas mortality rates showed a negative relationship. He attributed the higher growth rates and lower mortality during longer flooding periods to increased prey (benthic harpacticoid copepods) availability. Mummichogs had largely unrestricted access to prey only when the marsh surface was flooded, which was 16% to 32% of a given 24-h period depending on marsh elevation and tidal conditions. During low tide, mummichogs depleted prey resources in their aquatic microhabitats (i.e., small depressions on the marsh surface), although these resources were replenished with each new flood tide.

A prolonged hydroperiod also may indirectly benefit predators exploiting the marsh if it enhances their ability to forage or increases the productivity of prey species. Because plant stem density is inversely related to flooding duration, the vegetation is sparse in low marsh (West and Williams 1986; Mendelssohn and McKee 1988; Rozas and Reed 1993). Sparse vegetation may provide more foraging surface than unvegetated areas, yet may interfere less with the movement and foraging activity of predators than thick vegetation (Vince et al. 1976; Van Dolah 1978; West and Williams 1986).

Although high marsh is inundated infrequently and for shorter duration, this habitat is exploited by some natant species. During a rising tide, killifishes follow the advancing edge of flooding water across the marsh surface, so that at high tide they are concentrated in high marsh (Kneib 1976, 1984; Rozas and Reed 1993; Kneib and Wagner 1994). If the risk of stranding can be minimized, exploiting the high marsh may have several advantages. High marsh environments may contain more food than low marshes because prey are exposed to fewer predators and for shorter periods of time (Kneib 1984, 1993). High marshes also have denser vegetation and shallower water than low marshes, which may offer greater protection from predators. In addition, some resident estuarine species may spawn in high marsh. Selection of spawning habitat and timing of reproduction by these species are closely tied to hydroperiod (Taylor et al. 1979; Greeley and MacGregor 1983).

SUMMARY AND CONCLUSIONS

The relative importance of factors affecting marsh hydroperiod differ between the southeast Atlantic and northern Gulf coasts. Hydroperiods of most southeast Atlantic Coast salt marshes are driven by astronomical tides with a frequency of two flooding events per day. However, along most of the northern Gulf Coast, low-magnitude astronomical tides, which usually occur only once per day, are often overwhelmed by meteorological events, especially from late fall through early spring when cold fronts are common. In addition, other factors that affect coastal water levels or cause changes in surface elevation along both coasts have a greater effect on hydroperiod along the microtidal Gulf Coast.

Because daily flooding events in Gulf Coast marshes are greatly affected by meteorological forcing, the timing of marsh submergence in these marshes is less predictable than in Atlantic Coast marshes, where the hydroperiods are driven by regular astronomical tides. As a result, fewer species might be expected to use Gulf Coast marshes (less habitat utilization), especially organisms vulnerable to stranding, due to the unpredictable nature of marsh flooding there. However, a review of the few studies available indicates that similar numbers of species and higher densities of animals inhabit Gulf Coast marshes compared with Atlantic Coast marshes (Rozas 1993). The duration of marsh surface flooding seems to be more important than the predictability of habitat availability. At least some nekton species grow more slowly and experience higher mortality when their access to the marsh surface is limited (Weisberg and Lotrich 1982; Minello and Zimmerman 1991; Kneib 1993). Therefore, the productivity of some estuarine species may vary with changes in the degree of marsh flooding and habitat availability (Childers et al. 1990; Morris et al. 1990), but their existence is neither dependent on a constantly flooded marsh nor a predictable flooding regime.

Although portions of both coasts are experiencing accelerated rates of relative sea-level rise and salt-marsh deterioration, nowhere is this process occurring at a faster rate or on a grander scale than on the northern Gulf Coast in the Mississippi River deltaic plain. In southeastern Louisiana, large areas of salt marsh are exposed to unusually long periods of submergence. The hydroperiods of these marshes are thought to exceed the flooding tolerance of *S. alterniflora,* and consequently marshes are gradually undergoing vegetation deterioration and conversion to open water (Sasser et al. 1986; Mendelssohn and McKee 1988). The implication for nekton is that coastal submergence increases the percentage of time the habitat is available for use by lowering the marsh-surface elevation and increasing hydroperiod (Rozas and Reed 1993). When marshes deteriorate and fragment via this process, habitat access is also enhanced as the amount of marsh-water interface increases (Zimmerman et al. 1991). Most nektonic species and almost all fishery species that exploit the marsh surface in the southeast region of the United State use the marsh immediately adjacent to subtidal habitat to a much greater degree than interior marsh (Minello et al. 1991, 1994; Kneib and Wagner 1994; Peterson and Turner 1994).

Marshes affected by coastal submergence appear to be very productive, at least over the short term. Among the highest densities of nekton reported from studies of marsh-surface habitats are those documented from salt marshes undergoing coastal submergence (Zimmerman and Minello 1984; Rozas and Reed 1993). This process of gradual marsh submergence and deterioration may be important for maintaining the high productivity of species that use the marsh surface, some of which (e.g., penaeid shrimp) support valuable fisheries in the Gulf of Mexico. Zimmerman et al. (1991) attribute an increase in the production of penaeid shrimp and menhaden in the northern Gulf of Mexico over the last 20–30 yr to marsh fragmentation caused by coastal submergence. However, the productivity of species dependent on marshes can be sustained over the long term only if there is no significant loss in the total area of marsh habitat. In areas undergoing coastal submergence, the habitat base is sustainable only where losses are offset by marsh creation, for example, through delta-building processes. The formation of new marshes in coastal Louisiana, however, has been greatly curtailed by man interrupting the natural delta cycle of the Mississippi River. As a result, the total area of coastal marshes is declining (Dunbar et al. 1992). Freshwater environments are gradually being replaced by salt and brackish marshes (Chabreck and Linscombe 1982), and this may partially offset the loss of fishery habitat over the short term. However, continued degradation and reductions in the total area of primary fishery habitat will eventually lead to a reduction in the productivity of species dependent on coastal marshes (Zimmerman et al. 1991).

Most research on direct use of salt marshes by nekton is descriptive, and geographic coverage is limited. Although research on this topic is not extensive anywhere, most has been carried out along the northern Gulf Coast. A few studies of Atlantic Coast marshes have been published, but other than Chamberlain and Barnhart (1994), studies of natural marshes of the Pacific Coast are not available in the literature; therefore, comparisons between the Pacific Coast and other regions would be inappropriate to make at this time. Comparisons between the Gulf and Atlantic coasts must be considered only tentative at this time because studies conducted thus far have employed a variety of sampling methods in different marsh-surface microhabitats. More studies of habitat utilization are needed, especially on the Pacific and Atlantic coasts, and future investigations should include regional comparisons of similar marsh-surface microhabitats using identical quantitative sampling methods. Because habitat exploitation depends on marsh hydrology, hydroperiod data should be routinely collected in these studies. Currently, such data are rarely collected and reported in the literature.

Many questions about the influence of hydroperiod on habitat function remain unanswered for tidal salt marshes. A major difficulty is that hydroperiod affects many processes that also may indirectly influence habitat function. For example, hydroperiod affects the density and distribution of both plants and benthic infauna. But the abundance of some benthic infauna is related to vegetation distribution. All three factors (hydroperiod, benthic infauna, and vegetation) could influence nekton use of marsh habitat, and sorting out the relationships and elucidating the processes will not be easy. Carefully controlled experiments offer the best hope for elucidating all the mechanisms influencing habitat function.

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